THE ANIMAL HABITAT OF SOIL BACTERIA

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INTRODUCTION: THE DIRECT STUDY OF ANIMAL-BACTERIA RELATIONSHIPS

We, as biologists, have become accustomed to thinking of soil as an immensely complicated ecosystem. The invariable conclusion from biological studies is that soil is a heterogeneous system consisting of a large variety of biological habitats at varying successional stages. The application of sectioning techniques (Haarløv and Weis-Fogh, 1953; Alexander and Jackson, 1954; Hepple and Burges, 1956) indicates the spatial heterogeneity of solid, liquid and gas phases. Microbiological studies (Webster, 1956, 1957) have revealed fungal successions associated with rotting of the leaves of *Dactylis glomerata* indicating the extent of complexity which can arise through succession.

The lead given by Burges (1960) who drew attention to this outlook and by pioneers such as Kubiëna (1938, 1953) who first attempted to examine soil organisms *in situ* have lead to a variety of soil sectioning studies and to devices such as Tribe's baited slides (Tribe, 1960, 1961; Warcup, 1960), in an attempt to understand what really constitutes the habitat of a soil organism and how different kinds of organisms are spatially related to one another. A related approach is that of the Russian workers (Gabe, 1961; Aristovskaya and Parinkina, 1961; Foster, 1964) who have placed minute capillaries with optically flat surfaces in the soil. These are coated inside with various substrates including humic and fulvic acids and have become invaded by a range of micro-organisms whose existence, at least in the form described, had not been previously detected. They thrive in these very fine capillaries in a way which does not occur with dilution plates, Cholodny slides, etc.

A few animal biologists have also tried to penetrate the structural heterogeneity of the soil. The direct approach with the soil microscope has been limited because animals are mobile, but Haarløv and Weis-Fogh (1953) and Haarløv (1960) have used fairly thick sections of soil which was quickly frozen and then fixed in formalin vapour. These

have provided new information about the feeding habits and life histories of soil arthropods as well as the relations between their distribution and that of soil air spaces.

THE FUNCTIONAL STUDY OF SOIL PROCESSES

Whilst some attempt is being made to study soil organisms at an appropriate scale, other workers have been impressed with the need to quantify the processes of litter breakdown, chemical change and nutrient liberation which are going on in the soil. Some of these studies have been mainly concerned with rates of disappearance of litter usually placed on the soil surface in net bags or marked in such a way that the processes of breakdown can be followed quantitatively (Gilbert and Bocock, 1960; Bocock *et al.*, 1960; Cadwalladr, 1965; Crossley and Hoaglund, 1962; Witkamp, and Olson, 1963; Edwards and Heath, 1963). Another approach has been to assess the total respiratory activity involved in litter breakdown as measured by chemical analysis or calorimetry of the litter and by gas exchange due to successive groups of organisms. In this way the chemical pathways of decomposition can be followed and the relative roles of different groups traced (Bornebusch, 1930; Cragg, 1961; Macfadyen, 1963*a*, *b*; Nielsen, 1949, 1961; Phillipson, 1963). Comparable studies concerning the nitrogen cycle have been initiated (Satchell, 1963; Needham, 1957). A whole series of respiration studies by microbiologists has been reported (Birch and Friend, 1956; Bunt and Rovira, 1955*a*, *b*; Chase and Gray, 1953; Gaarder, 1957; Parkinson and Coups, 1963; Rovira, 1953; Witkamp, 1963). This work has given us a general insight into orders of magnitude to be expected and factors which influence the respiration rate, such as temperature, humidity, position in the profile and soil type. However, most measurements have been made with samples removed from the field and therefore subject to disturbance and often processed by air drying, grinding and other drastic measures.

It has been claimed (Parkinson and Coups, 1963), that the effect of sample removal is relatively trivial and that respiration rates soon revert to a steady level but there seems, in principle, much to be said for methods which can operate on undisturbed soil in the field. The idea of placing a container over a known area of soil and absorbing the carbon dioxide produced has long been considered and results reported by Wallis and Wilde (1957) confirmed suspicions that factors such as leakage, disturbance of the soil, respiration by higher plants and increased ventilation might produce excessively high readings. However,

the idea of sinking an open-ended cylinder in the soil some time before measurements begin and only sealing the upper end for the duration of the measurements has been exploited by Witkamp (1963 and personal communication) using a microdiffusion technique based on methods devized by Conway (1950) and Köpf (1952). An ingenious electrolytic titration method was used by the latter to determine CO_2 concentration in sub-samples of the confined air. I have used an apparatus similar to Witkamp's on soil under *Pteridium aquilinum* and have been struck by two features of the results. Firstly that there is a surprising degree of uniformity between adjacent samples and secondly, that when soil respiration figures are compared with primary plant production measure-

TABLE 1

Approximate comparisons of primary production and soil respiration in units of k cal./m.²/annum

Vegetation: region and type	Net Primary Production	Soil Respiration
Temperate: range	900–6,400[1]	—
Rough grazing	3,300[1]	—
Pteridium	4,050[1]	4,500[2]
Managed grassland	4,200[3]	4,500[4]
Arable	—	3,200[5] (2,900–11,000)[4]
Woodland	1,100–6,400[1]	6,900–10,600[4]
Equatorial forest (Congo)	30,000[6]	13,000–16,100[7]

Notes: Primary production is converted to equivalent CO_2 content on the basis: 5 k Cal./annum = 0·5 g. carbon/annum = 0·1 ml. CO_2/hr.

Daily soil respiration rates taken in summer at about 18°–20° have been roughly corrected to annual values by multiplying by $\frac{365}{2}$ (Nielsen, 1961).

The sources of the above figures are:
[1] Pearsall and Gorham (1956).
[2] Macfadyen unpublished.
[3] Macfadyen (1964).
[4] Russell (1950).
[5] Köpf (1952).
[6] Bray and Gorham (1964).
[7] Maldague and Hilger (1963).

ments there is a rather close correspondence between the two (Table 1).

A major criticism of this type of approach is that it ignores the microstructure of the soil by treating it as a uniform medium and frequently demands the application of highly unnatural treatments to the soil. Obviously we need a marriage between the purely descriptive approach which allows for the microscopic heterogeneity of soil on the one hand and the functional approach on the other, thus locating on a scale which is appropriate to soil structure the main centres of functional activity and measuring what is going on there. If I were able to report progress in this direction my topic of the animal habitat of soil bacteria would be

a relatively easy one, but since at the present time almost no progress has been made, I must content myself with pointing out a few promising approaches which may eventually lead to an understanding of the quantitative interrelations between the two groups.

THE INVERTEBRATE FAUNA OF SOIL

The biologist who attempts a census of small animals in the soil of a meadow or a deciduous wood is faced with a task so great that no one person has yet succeeded in covering all groups. A composite summary of such work from a variety of different studies, which will serve as a rough basis for discussion, is presented in Table 2. There are some hundreds of species of arthropods, represented by about one-third of a million individuals per square metre of soil. Nematodes occur in tens of millions per square metre and belong to 20 or so species.

TABLE 2

Table of numbers, biomass and respiration of main invertebrate groups in temperate grassland soil. Main sources are detailed in Macfadyen (1963a), supplemented by Phillipson (1963) and Duffey (1962). Note that since figures apply to normal populations in those places where the groups are found the total respiration of nearly 1400 K Cal. is two or three times too high

	Number of species	Number of individuals per m.^{2}	Biomass g./m.^{2}	Respiration K Cal./m.^{2}/annum
Protozoa	30	5×10^8	38	113
Nematoda	20	1×10^7	12	355
Lumbricidae	510	1×10^3	120	180
Enchytraeidae	<10	1×10^5	12	160
Mollusca	5	5×10^1	10	62
Myriapoda	5	5×10^2	12	96
Isopoda	3	5×10^2	5	38
Opiliones	5	1×10^2	0·7	55
Acari-				
Mesostigmata	25	5×10^3	1·0	64
Prostigmata	25	1×10^5	2·0	30
Oribatei	25	2×10^5	2·0	30
Araneae	90	6×10^2	6·0	34
Coleoptera	100?	1×10^2	1·0	8
Diptera	100?	2×10^2	1·0	6
Collembola	25	5×10^4	5·0	153

Tables of this kind, varying in completeness and accuracy, can be found in the works of Kevan (1962), Kühnelt (1961), Cragg (1961), Macfadyen (1963a), Franz (1943), Nielsen (1949, 1961) and Bornebusch (1930).

There are two features of such studies to which I want to refer: firstly, the comparative estimates of metabolic activity and secondly, the very great variations in the numbers of animals per sample unit. When the sampling areas are between 10 cm². and 100 cm²., it is invariably found that the variance exceeds the mean, implying a patchy (infradispersed or aggregated) distribution of the individuals within a species (Berthet, in the press).

It is apparent from a comparison of the animal respiration figures given in Table 2 with the total soil metabolism figures given in Table 1 that animal metabolism represents only some 10 per cent of the total (Macfadyen, 1961, 1963a). It follows that the remainder of the oxidation of organic matter must be due to micro-organisms. The low metabolic activity of the fauna might also be predicted from the failure of the pattern of total respiration to correspond with that of animal distribution; it is a common experience when sampling soil animals to find some samples with low counts of all species and others in which many species are abundant whilst soil respiration values remain very uniform.

Of course, the detection of pattern and of non-random distribution is highly dependent on the size of sample used (Pielou, 1957) and if it were possible to measure CO_2 output from small enough soil particles a patchiness might well be detected in this respect too. Also it must not be forgotten that animals are highly mobile and because, once sampled, an area is destroyed, we do not know how rapidly their distribution patterns change in time. A very limited amount of work has, however, been done on the mobility of individual soil animals and if the findings of Berthet (1964), using radioisotopes, are typical it seems likely that even the sluggish Oribatid mites normally move several centimetres in 24 hrs. and occasionally some tens of centimetres.

INTERACTION OF MICROBES WITH SOIL INVERTEBRATES

It would appear to follow from consideration of field sampling data that animal metabolism is low compared with total soil metabolism. On a centimetre scale animal dispersion is not reflected in a corresponding patchiness of soil respiration because the microbes (presumably mainly fungi in acid soils and bacteria in neutral and alkaline soils) dictate the gross pattern of biological activity in the soil.

A rather different impression is gained from the admittedly scanty and

purely qualitative evidence on the direct influences of animals and microbes on one another. In many cases such observations have been confined to fungi (Burges, 1965) but it seems likely that similar relationships with actinomycetes and bacteria will be detected.

Firstly there are well-developed bacterial floras in the guts of most soil invertebrates; for recent work see Healey (1965) on Collembola, Bocock (1963) on the millipede *Glomeris marginata* and Parle (1963*a*, *b*) on earthworms. The very considerable changes in the chemistry of food substances which occur during passage through these animals' guts (Gere, 1956, 1957; Bocock, 1963; van der Drift and Witkamp, 1959), indicate that conditions here are suitable for very high rates of chemical change. Further, animals such as the millipedes and earthworms consume and pass out an enormous amount of plant litter during the course of the year. Bocock has reported that up to 10 per cent of the total woodland litter may be consumed by a single species, *Glomeris*; Nielsen (personal communication) has reported higher figures for animals inhabiting limestone grassland. 'Moder' soils have been recognized by Kubiëna (1953) which consist almost entirely of faeces. Certainly in such cases the bacterial flora of invertebrate guts must play a most important role as a result of a symbiosis in which the animal provides not only suitable chemical and physical conditions but also a constant supply of well-titurated and moistened food.

Secondly, as has been recognized since the time of Darwin (1881), and pointed out by Russell (1950), soil animals, particularly those which are large and strong enough to make their own passages through the soil, produce a constant mixing of material from different layers of the soil and create channels which increase aeration and drainage of the soil. The effect of accidentally killing the larger species through excessive use of arsenic sprays has recently been reported by Raw (1962) who found that an anaerobic mor soil had been produced from a brown earth through such a treatment.

Thirdly, consequences of great importance to the development of microbial activity follow from the fact that animals are mobile. Witkamp (1960) has introduced small mites and collembola in glass tubes containing sterilized litter and shown how their movement through the medium can be followed by a trail of germinating spores. Most of these animals are armed with spines, bristles and sometimes scales and it needs little imagination to understand how spores can be spread, especially in the light of estimates of the mobility of Oribatid mites, normally thought of as being the most sluggish of soil animals (Berthet, 1964). Mobility must enhance enormously the chances of inoculating microhabitats

which are suitable for microbial development with both active forms, previously prevented from growth by shortage of substrate or by antibiotic substances, and also with spores whose germination depends on changes in environmental conditions.

Fourthly, we have the intriguing demonstration by Lingappa and Lockwood (1964) of a micro-succession in which the addition of fungus spores or their exudates to soil promoted bacterial growth and a several-fold increase in total soil respiration, apparently due to liberation of nutrients into the soil by the fungi. The growth of the bacteria was accompanied by liberation of a fungistatic substance and the decline of fungal spore germination. In the present context it is interesting to note that if such phenomena are at all general the presence of animals and their faeces are likely to stimulate bacterial growth in this, and perhaps other indirect ways.

Finally, of course, the animals themselves produce waste substances which are complementary to the needs of microbes. In the literature of soil microbiology it has been repeatedly emphasized that microbial decay is contingent on the supply of inorganic nutrients, particularly nitrates and phosphates. These are produced in abundance by animals in excreta and are also found in their corpses when they die. Both these sources of nutrients may be centres for the development of microbial colonies.

In short bacteria are characterized by the possession of an unparalleled repertoire of biochemical transformations. This repertoire is rarely exhibited to the full because the bacteria are not sufficiently mobile. Soil animals on the other hand are more uniform from a biochemical point of view but possess the one great asset of being able to move through the soil, carrying microbes with them on their bodies and inside their guts. Although there must be many variations on the same theme one can appreciate how bringing together the properties of the two groups results in a symbiosis between them and a great enhancement of the biological importance of both.

SOME SUGGESTIONS FOR AN EXPERIMENTAL APPROACH

I have shown (Macfadyen, 1964) that far more of the energy which terrestrial plants incorporate in the products of photosynthesis is liberated through organisms in the soil and litter than through herbivore food chains. How can we proceed if we are to gain an understanding of such a system which is remarkable both for the variety of species involved and the magnitude of its role in the total energy flow of terrestrial communities?

The content and flow of energy through different organisms remain the most generally applicable criteria by which we can select the most important pathways at the expense of the more trivial, but as the above considerations on the roles of soil animals demonstrate, the effectiveness of different organisms depends to a great extent on their biological idiosyncracies. The one animal characteristic of mobility, for instance, results in their disproportionate biological importance. Thus a relatively unimportant group, metabolically speaking, determines the level of respiratory activity of the microflora and therefore of the soil as a whole. We shall obviously have to try out a wide range of approaches to the general theme of detecting the catalytic effect of particular organisms on the system as a whole. One approach is through a much more detailed knowledge of life histories of soil organisms. There are at present whole groups, especially amongst the insect larvae and the mites, whose feeding habits are quite unknown. A combination of laboratory culture methods with soil sectioning and various kinds of field observation—including even the glass-lined underground observation chamber recently installed at East Malling—is indicated here. At present many protozoan and nematode species have been shown to feed on bacteria and some mites among the Tydaeidae, Scutacaridae and Oribatei are thought to do so, but none of these, as far as I am aware, have actually been cultured on bacteria, nor do we know anything about the specificity of their feeding habits.

A second approach is through the use of various kinds of baited traps such as the slides used by Tribe and others for stimulating growth of micro-organisms on particular substrates. This is a technically difficult and rather unrewarding method and should, perhaps, be supplemented by field experiments in which particular microbes are stimulated by the artificial addition of known substrates to the soil. Nevertheless, this method has provided badly needed direct evidence of feeding relations.

A third approach to the problem is the modification of field sites so as to select particular elements of the biota, using techniques which sterilize or repel certain organisms. These techniques include the use of chemical sterilizers and repellants, heat, cold and γ-radiation. All these treatments have undesirable features but almost nothing has yet been done to investigate their effects in different combinations and to trace the results of elimination and perhaps re-infestation of different groups of organisms. We have found that γ-irradiation is followed by a surprisingly rapid return of soil arthropods over a period of a few weeks and re-establishment of a microbial flora of a kind.

A fourth approach involves the use of artificial media such as air

dried, ground soil which has been re-wetted and either allowed to develop its own flora from spores or else inoculated with known microbes after sterilization. Such materials are characterized by clearly defined respiration regimes. Presumably the history of nutrient exploitation would also prove predictable. What would happen if, when the microflora has spored and become senescent, various members of the fauna were introduced? Obviously this approach, based on highly artificial substrates and ignoring natural soil structure, would demand very careful interpretation, but it offers the attractive attribute of repeatability and should throw light on information gained from more natural conditions.

Finally we must try to extend quantitative methods to a truly microscopical level: chemical methods and tracer techniques of fantastic sensitivity are now available and it is surely not impossible to apply them, in order, for instance, to study the exploitation of the nutrient reserves in the dead body or the faeces of a small soil arthropod, perhaps using the optically flat capillaries that were mentioned earlier.

The soil biologist is today faced with an embarrassingly rich variety of technical methods and a multitude of intriguing questions. I have tried to select some of both which are relevant to investigations of the relations between invertebrates and microbes because I believe this to be one of the key problems which faces us at present and one which could enormously enhance our understanding of the relevance of both groups of organisms to soil processes.

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